Fish assemblages in a mangrove shoreline lagoon of Guadeloupe (FWI): spatial and temporal distribution patterns along environmental gradients

by

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ABSTRACT. - Mangroves are recognized as important habitats for fish communities and serve as nurseries, feeding grounds or shelters. However, several studies have reported a worldwide regression of mangrove extent due to coastal management, land reclamation and wood cutting. Studies of fish assemblage patterns in mangroves are needed in order to understand the processes structuring fish communities and to evaluate the influence of environmental or anthropogenic changes on these distributions. Fish were collected with nets in 32 stations in the mangrove shoreline lagoon of the Grand Cul-de-Sac Marin (Guadeloupe, Lesser Antilles) during dry and wet seasons. A set of 21 environmental descriptors was recorded in each mangrove site in order to identify and explain spatial and temporal patterns of fish assemblages. A total of 106 fish species belonging to 44 families were recorded. Canonical analyses and classifications revealed the presence of four fish assemblages distributed along a gradient oriented from the coastal mangrove seawards. This environmental gradient was related to several variables, such as coral reef or river proximities, water transparency and salinity. It opposed fish communities dominated by either mangrove or coral reef fish species. Variation partitioning showed that physical, chemical and geographical descriptors were the most important variables, but thus accounted for only 29.6% of mangrove fish abundance variation. Considering trophic categories, second order carnivorous and omnivorous fishes dominated in biomass in river mouth stations, whereas first order carnivorous and piscivorous species dominated in mangrove areas close to coral reefs and seagrass beds. These differences in the structure of trophic categories among mangrove shoreline habitats suggest that food availability plays an important role in the structure of the mangrove fish communities, in addition to abiotic factors and the presence of neighbouring habitats, such as coral reefs or seagrass beds.

RÉSUMÉ. - Distributions spatiale et temporelle des communautés ichtyologiques dans une mangrove de Guadeloupe (Antilles françaises) : relation avec les variables environnementales.

L'écosystème de mangrove est considéré comme un habitat important pour les communautés de poissons en tant que nurserie, zone d'alimentation ou abris. Cependant, plusieurs études ont révélé une régression mondiale des surfaces de mangrove due à des aménagements côtiers pour l'agriculture, pour des constructions, et due à la déforestation. Des études sur les distributions des communautés de poissons en mangrove sont nécessaires pour comprendre les phénomènes qui déterminent la structure de ces communautés et pour évaluer l'influence des changements environnementaux ou anthropiques sur ces distributions. Les poissons ont été capturés à l'aide de filets dans 32 stations de la bordure de mangrove du lagon du Grand Cul-de-Sac Marin (Guadeloupe, Antilles françaises) en saison sèche et en saison des pluies. Un ensemble de 21 variables du milieu ont été mesurées afin d'expliquer les distributions des peuplements. Au total, 106 espèces appartenant à 44 familles ont été identifiées. Des analyses canoniques et des classifications hiérarchiques ont permis de mettre en évidence quatre groupes d'espèces distribués le long d'un gradient environnemental orienté de la côte vers la barrière récifale corallienne. Ce gradient est relié à la proximité du récif et des embouchures de rivières, la transparence de l'eau et la salinité. Il sépare des peuplements de poissons dominés par des espèces de mangrove d'autres composés d'espèces récifales. Une partition de la variance par analyse canonique a montré que les facteurs physiques et chimiques et les variables géographiques permettent d'expliquer 29,6% de la variance des données d'espèces exprimées en effectifs. Considérant les catégories trophiques, les carnivores du second ordre et les omnivores dominent en biomasse dans les sites de mangrove situés à proximité des rivières, alors que les piscivores et les carnivores du premier ordre sont prépondérants dans les stations proches des récifs coralliens et des herbiers. Ces différences observées dans les compositions des catégories trophiques suggèrent que les disponibilités des ressources alimentaires jouent également un rôle important dans la structure des communautés de poissons en mangrove.

Key words. - Fish assemblage - Lesser Antilles - Guadeloupe - Mangrove - Spatial and temporal patterns - Environmental variables.

Mangrove ecosystems represent important habitats for fish communities and serve as nurseries for juveniles (Bell *et al.,* 1984; Laegdsgaard and Jonhson, 2001; Nagelkerken and van der Velde, 2002), as feeding grounds (Odum and Heald, 1975; Sheaves and Molony, 2000) or as shelters (Rooker and Dennis, 1991; Nagelkerken *et al.,* 2000). How-

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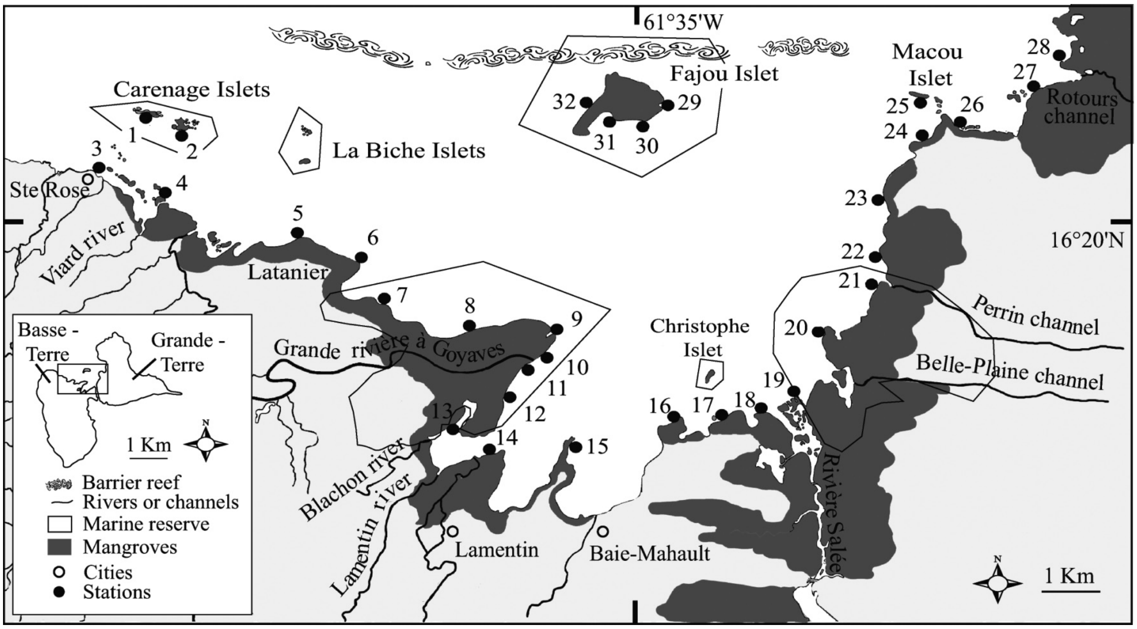

Figure 1. - Mangrove sampling sites (●) in the GCSM lagoon in Guadeloupe (FWI, Caribbean).

ever, during the last two decades, the surfaces of mangrove in the world have been reduced by 20% (FAO, 2007). With this important global loss, mainly due to bad coastal management, land reclamation and wood cutting, mangroves are considered as one of the world's most threatened tropical ecosystem (Valiela *et al.,* 2001). Against this alarming background, there is now an increasing concern for a sustainable management of mangrove ecosystems and a need to better understand the relationships between mangrove habitats and their associated fishes (Blaber, 2007).

Within mangrove habitats, several environmental factors are known to influence fish assemblages, such as salinity, temperature or turbidity (Cyrus and Blaber, 1987; Ley *et al.,* 1999; Serafy *et al.,* 2003). In the Caribbean, mangroves are often adjacent to seagrass beds and coral reefs and this spatial arrangement may influence the structure of fish communities (Claro and Garcia-Arteaga, 1993; Nagelkerken *et al.,* 2000; Nagelkerken and van der Velde, 2002). Proximities of such marine ecosystems should therefore be taken into account when assessing the composition, as well as spatial and seasonal patterns of mangrove fish assemblages.

In Guadeloupe Island (Lesser Antilles), mangrove ecosystems cover an area around 3 000 hectares, the largest mangrove surface in the Lesser Antilles (Ellison and Farnsworth, 1996; Chauvaud *et al.,* 2001). Based on fish assemblage composition and structure, Louis (1983) has identified different mangrove systems in Guadeloupe: the lagoon system (consisting of lagoons enclosed by mangroves); the channel system (composed by channels and rivers) and the shoreline system (represented by the mangrove fringe bordering the coast). Apart from the researches of Baelde (1990), who studied the fish communities in two mangrove islets, no study has yet focused on fish assemblages observed among the entire mangrove shoreline system in Guadeloupe and their relationships with environmental variables.

Thus, the aims of the present study were: 1) to determine the spatial and seasonal patterns of mangrove shoreline fish assemblages; 2) to identify their relationships with environmental descriptors; 3) to characterize the relative contribution of physical, chemical, spatial and temporal descriptors to fish distribution and 4) to assess the influence of environmental variables on fish feeding guild composition and structure.

MATERIAL AND METHODS

Study sites and sampling

Around 80% of mangroves present in Guadeloupe are located around the bay of the Grand Cul-de-Sac Marin (GCSM), a lagoon of 11,000 hectares (Chauvaud *et al.,* 2001) (Fig. 1). The GCSM bay is bordered by red mangroves (*Rhizophora mangle*) and is limited seawards by a 30 km long barrier reef (Bouchon and Laborel, 1990). The lagoon floor is diverse and includes numerous coral formations near mangrove islets, sandy and muddy substrates near mangroves which can be colonized by seagrass beds (8200 ha; Chauvaud *et al*., 2001), composed mainly by *Thalassia testudinum* and *Syringodium filiforme*. A detailed map showing the location of seagrass beds in the GCSM bay is presented in Chauvaud *et al*. (2001). A total of 32 stations were sampled along the whole mangrove fringe of the GCSM from

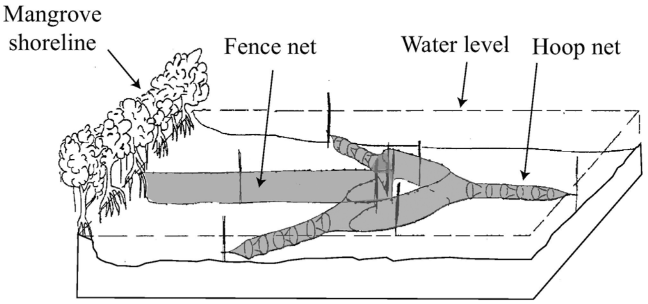

Figure 2. - The fishing net "capéchade" used for sampling in mangrove.

Sainte-Rose on the west to Rotours channel on the east and included the mangrove islets of Carenage, Fajou and Macou (Fig. 1). The sampling focused in the mangrove shoreline due to the lack of data in this mangrove system. These stations, with depth between 0.5 and 1 m, were chosen for their different configurations, such as the presence-absence of seagrass beds, the proximity of coral formations or rivers and the mangrove islets. In the same way, four sites were chosen around Fajou islet according to the presence (sites 30, 31) or absence (site 29) of seagrass beds and proximity to coral reefs (sites 29 to 32). The 32 mangrove sites and the proximity to coral reefs were sampled once during the dry season and once during the wet season of 2005.

Fishes were collected with a hoop net called capéchade (Fig. 2). This fishing gear is composed by a fence net (50 m long; 2 m high; mesh size: 13.8 mm) which is set perpendicularly to the mangrove shoreline and deviated the fish migrating along the shore in three hoop nets of decreasing mesh size (8 to 6 mm) (Fig. 2). This fishing net was already used in the French West Indies and is well adapted to shallow and turbid environment, allowing the capture of small transient species as well as mangrove resident fishes (Lasserre and Toffart, 1977; Louis, 1983; Louis *et al*., 1992). The net was set in the morning and lifted 24 hours later. Fishes were then identified to the species level, counted, measured and weighted. The length at sexual maturity reported in the literature was used to separate juveniles from adult fishes (Cervigón, 1991, 1993, 1994; García-Cagide *et al*., 1994; Froese and Pauly, 2009).

In each station, 21 environmental descriptors were measured: physical and chemical variables (temperature, salinity, pH, dissolved oxygen, suspended materials, water transparency, nitrates, phosphates, chlorophyll$_a$, pheophytin$_a$, rainfall), spatial descriptors (reef and river proximities, location inside or outside a marine reserve), habitat descriptors (mangrove and forest extent facing each station), presence or absence of seagrass beds on the bottom, water motion (calm or turbulent), geographical location (latitude, longitude) and the seasons (dry or wet season). Physical and chemical variables were measured in the morning, between 9 and 10 am. Among these variables, 4 are qualitative binomial variables (protection status, seagrass beds, water motion and season).

Fish species were classified among the six trophic categories as defined by Bouchon-Navaro *et al*. (1992) from data reported in the literature (Randall, 1967; Claro, 1994): herbivores (He) consuming algae and plants, omnivores (Om) which feed on benthic invertebrates and more than 10% of algae, zooplankton feeders (Pl), first order carnivores (C1) consuming mainly invertebrates, second order carnivorous fishes (C2) ingesting fish and benthic invertebrates and piscivorous ones (Pi) consuming more than 80% of fishes.

Statistical analyses

Canonical correspondence analyses (CCA) were performed, using the software CANOCO (ter Braak, 1988), to identify the associations between fish assemblages and environmental descriptors influencing their distribution. CCA is a method which optimizes the relationships between the species distribution and a linear combination of environmental variables (ter Braak and Verdonschot, 1995). In order to downweigh large numbers of taxa per station, abundance and biomass data sets were log transformed before canonical analyses, in order to reduce the effects of abundant species on assemblage patterns. The statistical significance ($p < 0.05$) of the effect of each variable was tested by the permutation test of Monte Carlo (ter Braak, 1992).

Variance partitionings were applied to estimate the relative importance of environmental variables organized into three groups: physical and chemical, spatial and seasonal descriptors (Borcard *et al.,* 1992). This method enables to determine the contribution of one set of variables while the other groups of descriptors act as covariables (Borcard *et al.,* 1992; Anderson and Gribble, 1998). Results of variation partitioning were based on Ezekiel's adjustment of variation as recommended by Peres-Neto *et al*. (2006).

The results of canonical analyses were completed with hierarchical clusterings, which facilitate the identification of fish groups from the projection on the canonical biplot. Clusters were performed using the Progiciel R and were calculated using Ward algorithm and Euclidian distance on the sample scores produced by the factorial analysis as suggested by Roux (1985). The Kendall coefficient of concordance was used to identify fish species, which are significantly associated to each group identified by hierarchical clusterings (Legendre, 2005).

Non-parametric tests of comparisons (Kruskal-Wallis and Wilcoxon signed-rank tests) were performed to compare fish and environmental data between both seasons because these tests do not assume a multinormal distribution of the data (Legendre and Legendre, 1998).

RESULTS

In the GCSM, a total of 106 species belonging to 44 families were observed along the mangrove shoreline (Tab. I). Haemulidae (8 species), Gerreidae (7 species) and Lutjanidae (7 species) were the most representative families in terms of diversity. Mean species richness per station was 19.2 ± 1.4, mean abundance 1868.7 ± 703.5 individuals and mean biomass 13.5 ± 3.2 kg per sampling. Species richness, abundance and biomass did not differ significantly between seasons (Wilcoxon signed-ranked test; $p > 0.05$). In terms of abundance, six species dominated the community and accounted for 86% of the total number of fish collected: *Jenkinsia lamprotaenia*, *Harengula clupeola, Diapterus rhombeus*, *Atherinomorus stipes, Anchoa lyolepis* and *Anchoa hepsetus*. Each of all the remaining fish species represent less than 3% of the total fish abundance. In terms of families, four families (Clupeidae, Engraulidae, Gerreidae and Mugilidae) gathered 94% of the total number of fishes and each of all the remaining families represented less than 3% of total abundance.

Five species accounted for 56% of the total fish biomass: *Diapterus rhombeus, Dasyatis americana, Archosargus rhomboidalis, Bairdiella ronchus* and *Harengula clupeola* (Tab. I). Concerning biomass, five families accounted for 68% of the total biomass, i.e., Gerreidae, Dasyatidae, Sparidae, Clupeidae and Sciaenidae (Tab. I).

Fish assemblages and influence of environmental variables

Twenty four rare species, represented by only one specimen, were excluded from the analyses (Tab. I). Thus, hierarchical and canonical analyses were performed on 82 fish species. CCA were performed between "sites by species" and "sites by environmental factors" matrices. Each matrix, expressed in presence-absence, numerical abundance and biomass, was analyzed separately. The overall permutation tests and the test on the first canonical axis were statistically significant for the three analyses ($p < 0.001$). Moreover, the variance explained by the first two canonical axes was higher for fish abundance (35.4%) compared to biomass (27.3%) or presence-absence (24.2%) data sets. Thus, results obtained

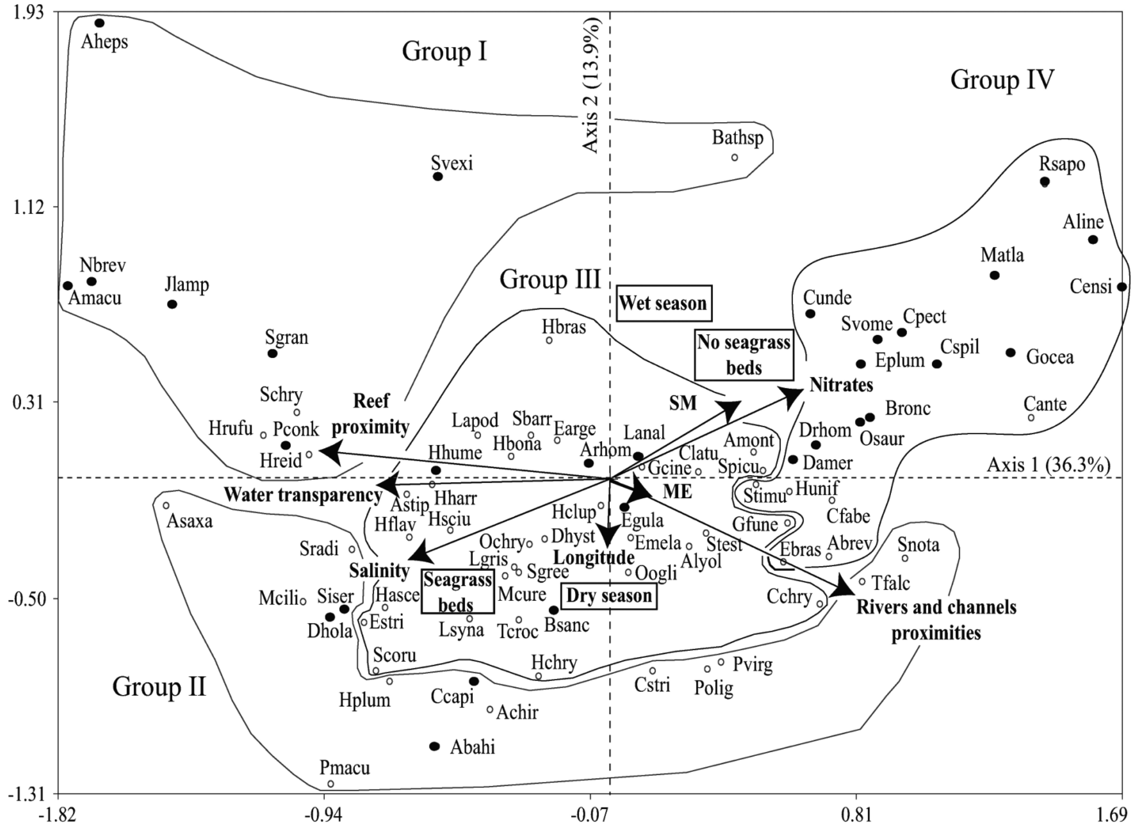

Figure 3. - Projection of the fish assemblages on the first two axes determined by the canonical correspondence analysis (CCA). Significant environmental variables and fish species with relative occurrence higher than 3% are projected on the CCA biplot. Quantitative descriptors are represented by arrows and qualitative variables by their centroids. The four fish assemblages identified by classifications are reported on the biplot. Significant fish species identified by Kendall coefficient of concordance are represented by a black dot. M.E., Mangrove extent; S.M., Suspended materials. Species codes are given in table I.

Table I. - Relative occurrences (%), abundance (%) and biomass (%) of fish species observed in the GCSM. Rare species are represented by an asterisk (*). Trophic categories (TC) are given: Pl, Planktivores; He, Herbivores; Om, Omnivores; C1, First order carnivores; C2, Second order carnivores; Pi, Piscivores. Ecological categories (EC): M (mangrove species), S (seagrass beds species), R (reef fish species). The species codes used in ordination analysis (Fig. 3) are added.

Families	Species	Species code	Dry and wet seasons				
			Occurrence (%)	Abundance (%)	Biomass (%)	TC	EC
Carcharhinidae	*Negaprion brevirostris*	Nbrev	6.8	0.005	3.958	Pi	R
Dasyatidae	*Dasyatis americana*	Damer	22.0	0.024	12.335	C2	RSM
Megalopidae	*Megalops atlanticus*	Matla	11.9	0.010	0.458	C2	RM
Muraenidae	*Gymnothorax funebris*	Gfune	32.2	0.029	4.232	Pi	RSM
	Lycodontis vicinus *	Lvici	1.7	0.001	0.063	Pi	R
Ophichthidae	*Ophichthus* cf. *Ophichthus parilus* *	Opari	1.7	0.001	0.028	C2	SM
Engraulidae	*Anchoa hepsetus*	Aheps	6.8	6.669	0.829	Pl	M
	Anchoa lyolepis	Alyol	81.4	8.168	1.997	Pl	M
	Anchoviella brevirostris	Abrev	8.5	0.075	0.287	Pl	M
Clupeidae	*Harengula clupeola*	Hclup	86.4	21.012	8.900	Pl	RSM
	Harengula humeralis	Hhume	55.9	1.023	0.521	Pl	RSM
	Jenkinsia lamprotaenia	Jlamp	20.3	32.343	2.285	Pl	RS
	Opisthonema oglinum	Oogli	23.7	0.521	0.328	Pl	M
Carapidae	*Carapus bermudensis* *	Cberm	1.7	0.001	< 0.001	C2	SM
Mugilidae	*Agnostomus monticola*	Amont	3.4	0.002	0.026	C1	SM
	Mugil curema	Mcure	35.6	1.930	1.066	Om	SM
Atherinidae	*Atherinomorus stipes*	Astip	71.2	8.979	1.961	Pl	RSM
	Hypoatherina harringtonensis	Hharr	3.4	0.036	0.007	Pl	RSM
Belonidae	*Strongylura notata*	Snota	3.4	0.006	0.028	Pi	SM
	Strongylura timucu	Stimu	11.9	0.020	0.106	Pi	M
	Tylosurus crocodilus	Tcroc	16.9	0.013	0.457	Pi	RSM
Hemiramphidae	*Hemiramphus brasiliensis*	Hbras	3.4	0.004	0.037	Om	SM
	Hyporhamphus unifasciatus	Hunif	23.7	0.447	0.429	Om	SM
Holocentridae	*Holocentrus adscensionis*	Hadsc	10.2	0.007	0.060	C1	R
	Holocentrus rufus	Hrufu	15.3	0.024	0.199	C1	R
	Myripristis jacobus *	Mjaco	1.7	0.001	< 0.001	Pl	R
	Sargocentron coruscum	Scoru	20.3	0.089	0.015	C1	R
	Sargocentron vexillarium	Svexi	3.4	0.005	0.003	C1	R
Syngnathidae	*Hippocampus reidi*	Hreid	3.4	0.002	< 0.001	C1	RS
Scorpaenidae	*Scorpaena grandicornis*	Sgran	6.8	0.004	0.031	C2	R
	Scorpaena inermis *	Siner	1.7	0.001	0.000	C2	R
Centropomidae	*Centropomus ensiferus*	Censi	10.2	0.201	0.718	C2	M
	Centropomus parallelus *	Cpara	1.7	0.001	0.017	C2	M
	Centropomus pectinatus	Cpect	20.3	0.047	0.290	C2	M
	Centropomus undecimalis	Cunde	23.7	0.026	1.990	C2	M
Serranidae	*Epinephelus striatus*	Estri	3.4	0.003	0.039	C2	RS
	Rypticus saponaceus	Rsapo	5.1	0.003	0.018	C2	RSM
Apogonidae	*Apogon maculatus*	Amacu	3.4	0.002	0.001	Pl	R
	Phaeoptyx conklini	Pconk	8.5	0.007	0.001	Pl	R
	Phaeoptyx pigmentaria *	Ppigm	1.7	0.001	< 0.001	Pl	RS
Echeneidae	*Echeneis naucrates* *	Enauc	1.7	0.001	0.002	C2	R

Table I. - Continued.

Families	Species	Species code	Dry and wet seasons				
			Occurrence (%)	Abundance (%)	Biomass (%)	TC	EC
Carangidae	*Caranx latus*	Clatu	76.3	0.425	1.192	Pi	RSM
	Chloroscombrus chrysurus	Cchry	8.5	0.036	0.011	C1	SM
	Oligoplites saurus	Osaur	28.8	0.092	0.069	Pi	SM
	Selene vomer	Svome	11.9	0.009	0.020	C2	RM
	Trachinotus falcatus	Tfalc	5.1	0.003	0.001	C1	M
Lutjanidae	*Lutjanus analis*	Lanal	11.9	0.007	0.152	C2	RM
	Lutjanus apodus	Lapod	23.7	0.027	0.557	C2	RM
	Lutjanus cyanopterus *	Lcyan	1.7	0.001	0.009	C2	SM
	Lutjanus griseus	Lgris	23.7	0.018	0.143	C2	RSM
	Lutjanus jocu *	Ljocu	1.7	0.001	0.038	C2	SM
	Lutjanus synagris	Lsyna	10.2	0.007	0.033	C2	RSM
	Ocyurus chrysurus	Ochry	18.6	0.043	0.072	C2	RS
Gerreidae	*Diapterus rhombeus*	Drhom	64.4	9.498	13.898	Om	SM
	Eucinostomus argenteus	Earge	55.9	0.569	0.451	C1	SM
	Eucinostomus gula	Egula	88.1	2.742	3.312	C1	SM
	Eucinostomus melanopterus	Emela	22.0	0.037	0.104	C1	M
	Eugerres brasilianus	Ebras	22.0	0.033	0.669	C1	M
	Eugerres plumieri	Eplum	40.7	0.128	2.307	C1	M
	Gerres cinereus	Gcine	74.6	0.461	1.060	C1	RSM
Haemulidae	*Haemulon bonariense*	Hbona	25.4	0.017	0.153	C1	M
	Haemulon chrysargyreum	Hchry	16.9	0.036	0.057	C1	RSM
	Haemulon flavolineatum	Hflav	30.5	0.047	0.077	C1	RSM
	Haemulon parrai *	Hparr	1.7	0.001	0.003	C1	RSM
	Haemulon plumieri	Hplum	6.8	0.006	0.021	C1	RSM
	Haemulon sciurus	Hsciu	40.7	0.062	0.608	C1	RSM
	Pomadasys croco *	Pcroc	1.7	0.001	0.062	C2	M
	Pomadasys corvinaeformis *	Pcorv	1.7	0.001	0.044	C2	M
Sparidae	*Archosargus rhomboidalis*	Arhomb	86.4	0.954	12.209	Om	RSM
Polynemidae	*Polydactylus oligodon*	Polig	11.9	0.015	0.033	C2	M
	Polydactylus virginicus	Pvirg	13.6	0.015	0.040	C2	M
Sciaenidae	*Bairdiella ronchus*	Bronc	52.5	2.171	9.440	C2	M
	Bairdiella sanctaluciae	Bsanc	8.5	0.014	0.090	C2	M
Mullidae	*Pseudupeneus maculatus*	Pmacu	3.4	0.002	0.001	C1	RS
Chaetodontidae	*Chaetodon capistratus*	Ccapi	16.9	0.016	0.005	C1	R
	Chaetodon ocellatus *	Cocel	1.7	0.001	< 0.001	C1	R
	Chaetodon striatus	Cstri	3.4	0.006	< 0.001	C1	R
Pomacentridae	*Stegastes leucosticus* *	Sleuc	1.7	0.001	< 0.001	Om	RS
	Stegastes variabilis *	Svari	1.7	0.001	0.001	Om	RS
	Abudefduf saxatilis	Asaxa	5.1	0.005	0.019	Om	RS
Cichlidae	*Oreochromis mossambicus* *	Omoss	1.7	0.001	0.015	Om	M
Labridae	*Halichoeres bivittatus* *	Hbivi	1.7	0.001	0.002	C1	RS
	Lachnolaimus maximus *	Lmaxi	1.7	0.001	0.010	C1	RS
Scaridae	*Scarus iserti*	Siser	3.4	0.002	0.001	He	RS
	Sparisoma chrysopterum	Schry	3.4	0.003	0.024	He	RS
	Sparisoma radians	Sradi	11.9	0.023	0.045	He	RS

Table I. - Continued.

Families	Species	Species code	Dry and wet seasons				
			Occurrence (%)	Abundance (%)	Biomass (%)	TC	EC
Tripterygiidae	*Labrisomus gobio* *	Lgobi	1.7	0.001	0.001	C2	M
Gobiidae	*Bathygobius* sp.	Bathsp	5.1	0.003	< 0.001	C1	M
	Gobionellus oceanicus	Gocea	8.5	0.053	0.054	C1	M
	Lophogobius cyprinoides *	Lcypr	1.7	0.001	< 0.001	C1	M
Ephippidae	*Chaetodipterus faber*	Cfabe	3.4	0.004	0.004	C1	RM
Acanthuridae	*Acanthurus bahianus*	Abahia	15.3	0.038	0.005	He	RS
	Acanthurus chirurgus	Achir	8.5	0.034	0.0107	He	RS
Sphyraenidae	*Sphyraena barracuda*	Sbarr	67.8	0.090	1.810	Pi	RSM
	Sphyraena picudilla	Spicu	11.9	0.008	0.026	Pi	RSM
Scombridae	*Scomberomorus regalis* *	Srega	1.7	0.001	0.006	C2	RS
Paralichthyidae	*Citharichthys spilopterus*	Cspil	18.6	0.027	0.047	C2	M
Achiridae	*Achirus lineatus*	Aline	5.1	0.017	0.083	C2	SM
Monacanthidae	*Monacanthus ciliatus*	Mcili	3.4	0.002	0.001	Om	RS
	Stephanolepis setifer *	Sseti	1.7	0.001	< 0.001	C1	R
Ostraciidae	*Lactophrys trigonus* *	Ltrig	1.7	0.001	0.026	C1	R
Tetraodontidae	*Sphoeroides greeleyi*	Sgree	50.8	0.159	0.410	C1	MS
	Sphoeroides testudineus	Stestu	66.1	0.267	2.453	C1	MS
Diodontidae	*Chilomycterus antennatus*	Cante	3.4	0.002	0.021	C1	RSM
	Diodon holacanthus	Dhola	3.4	0.002	0.053	C1	RSM
	Diodon hystrix	Dhyst	10.2	0.008	4.207	C1	RSM

from CCA, clusters analyses and variation partitioning will be presented thereafter with data on fish abundance.

The two canonical axes gathered 35.4% of the information present in the data set of fish abundance (axis 1: 36.3%; axis 2: 13.9%) (Fig. 3). Out of 21 variables introduced in the analysis, 10 descriptors were significantly correlated to fish abundance (Fig. 3). Canonical coefficients indicate that seven environmental variables were correlated to the first axis. They opposed, on one side, mangroves close to the barrier reef (-0.85) with more transparent (-0.70), salty waters (-0.61) and the presence of seagrass beds (-0.43), to sites influenced by channel or rivers proximity (0.73) on the other side, high concentrations of nitrates (0.58) and suspended materials (0.38), the absence of seagrass beds (0.43) and large extent of mangroves in front of the sampling station (0,12). The second axis is significantly associated with the dry (-0.47) and wet (0.47) seasons and with an east-west gradient across the lagoon (-0.22) (Fig. 3).

Fishes were arranged by the CCA analyses according to their preferences towards the significant environmental variables. Complementary cluster analyses separated four groups of fish species reported on the CCA biplot. In each group, the species significantly linked by the computation of the concordance coefficient of Kendall are presented with a black dot (Fig. 3). On the left side of the first CCA axis, the first group (I) is dominated, in terms of abundance, by reef species: *Scorpaena grandicornis, Apogon maculatus, Negaprion brevirostris, Sargocentron vexillarium* or *Phaeoptyx conklini*. These species were observed in the mangrove stations of Fajou and Macou islets, located near the barrier reef, which are characterized by more transparent, salty waters and the presence of seagrass beds (Fig. 3). On the other side of this first axis, group four (IV) gathers fish species observed in mangrove sites influenced by the proximity of rivers and channels mouths and characterized by fresh, turbid waters, higher nitrate concentrations and the absence of seagrass beds. This fish assemblage is composed of mangrove resident species (*Bairdiella ronchus*), mangrove-associated species (*Centropomus undecimalis*) and species found in the mangrove during their reproduction, *Gobionellus oceanicus* (Louis, 1983) (Fig. 3).

In the centre of the graph, the group number three (III) is composed of species widely distributed over the GCSM lagoon neither influenced by reef nor by rivers proximities (Fig. 3). These species can indifferently be observed in mangrove or seagrass beds: *Eucinostomus gula*, *Archosargus rhomboidalis, Bairdiella sanctaluciae*. Several juvenile reef species also belonged to that group, such as: *Lutjanus analis, Ocyurus chrysurus, Caranx latus* and *Epinephelus striatus* (Fig. 3).

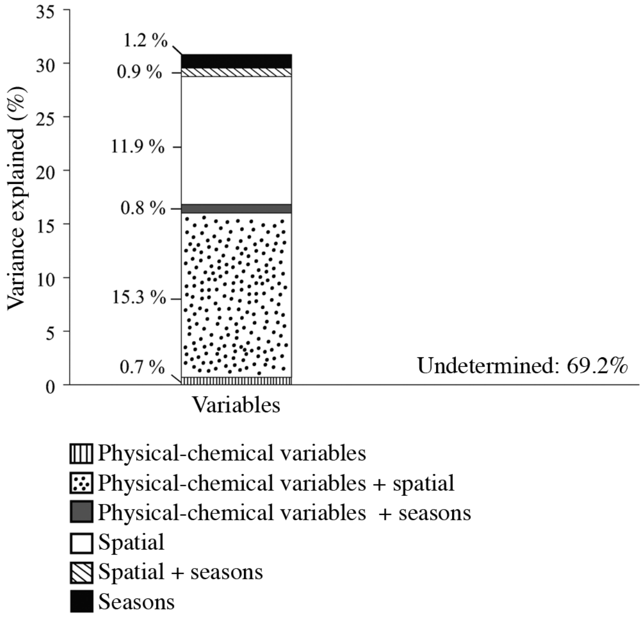

Figure 4. - Variation partitioning of the fish abundance data matrix among sets of explanatory variables: physical and chemical, physical, chemical variables spatially structured, physical, chemical variables seasonally structured, spatial descriptors, spatial descriptors seasonally structured and seasons.

The second axis is correlated to the season and an East-West gradient. The second group of species (II) includes both reef and seagrass species, *Acanthurus bahianus, Chaetodon capistratus*, *Scarus iserti*, *Diodon holacanthus*, as well as mangrove resident species, *Polydactylus oligodon*, *P. virginicus*. This group of fishes is observed during the dry season in the westward stations of Carenage islets and Ste Rose (Group II), characterized by more saline and transparent waters, the presence of seagrass beds mixed with mangrove prop-roots, several live corals near the mangrove shoreline in islets as well as the influence of rivers near Ste Rose (Figs 1, 3). The proximity of both river mouths and coral reef can explain the diversity of the fish assemblage observed in these mangrove sites.

Figure 4 presents the results of the variation partitioning performed on fish abundance data and three sets of variables: spatial (longitude, reef and rivers proximities, mangrove extent, the presence or absence of seagrass beds), physical and chemical (salinity, suspended materials, water transparency and nitrates), and seasons (dry or wet season). Together, these factors explained 30.8% of the variance of the fish distribution (Fig. 4). The difference in the amount of variance explained between CCA (35.4%) and variation partitioning (30.8%) is due to the Ezekiel's adjustment performed in variation partitioning which enabled to correct fractions of variation depending on the different number of environmental descriptors present in each set of variables (Peres-Neto *et al.,* 2006). Spatial descriptors and physical-chemical variables explained respectively 28.1% and 16.8% of the variance. The seasons accounted for the lowest amount of the variation (2.9%) (Fig. 4).

The measurements of significant physical and chemical variables among the different groups of mangrove stations showed a spatial pattern for the values of these descriptors (Tab. II, Fig. 5). Salinity and water transparency decrease from mangrove islets stations located near the barrier reef to mangrove sites located near rivers and channels mouths ($p < 0.0001$, Kruskal-Wallis non-parametric test). Conversely, suspended materials and nitrate concentrations increased towards the mangrove coasts ($p < 0.05$, Kruskal-Wallis non-parametric test) (Tab. II, Fig. 5). A Kruskal-Wallis test revealed that salinity and nitrate concentrations were the main variables responsible for seasonal differences ($p < 0.0001$) (Tab. II). Moreover, the spatial pattern observed in the values of physical and chemical descriptors can explain the part of the variance (15.3% only) which is shared by both spatial, physical and chemical variables in the variation partitioning results (Tab. II, Fig. 4).

Trophic categories

The relative proportions of the six trophic categories are described in abundance and biomass for the four groups of stations identified from hierarchical classification (Fig. 5, Fig. 6). Considering abundance, a decrease in the number of planktivorous species is observed from the mangrove islets "Fajou and Macou Islets" (96.8%) and "Carenage Islets-Ste Rose" (77.2%), located near the barrier reef, to the mangrove sites close to river and mouths (12.9%). Conversely, an increase in the proportion of omnivores (from 0.9% to 53.0%) and second order carnivores (from 0.2% to 23.0%) occurred from the reefal stations of "Fajou and Macou Islets" to river and channels mouths stations (Fig. 6).

The differences among the trophic structure of the mangrove fish assemblages are more obvious in terms of biomass (Fig. 6). The biomass of planktivores is around 22% in the three first groups of stations and decrease to 3.1% in the river mouths sites. The proportion of omnivores is relatively important in all the group of stations, with relative biomass comprised between 15.7% in Carenage-Ste Rose stations and 33.6% in the typical mangrove shoreline sites. Second order carnivores dominate in the river mouths stations (54.7%) and their proportion decrease to the reefal sites (9.3%). The inverse trend is observed for piscivorous fishes, which are present in higher proportions in the mangrove islets of Fajou and Macou (30.2%). The relative biomass of first order carnivores is less than 16% in the different stations except in the group "Carenage Islets-Ste Rose" where it reaches 30.9% (Fig. 6).

For both abundance and biomass, herbivorous fishes are poorly represented in all the mangrove stations, with a maxi-

Table II. - Mean values (± IC) of the four significant physical and chemical variables between the different groups of mangrove stations identified by the hierarchical classifications (Fig. 3). * p < 0.05 while testing the difference between Group I, Group II and Groups III-IV.

Variables	Mean values (±SD)		Wilcoxon signed-rank test	Groups of stations				Kruskal-Wallis test
	Dry season	Wet season		Fajou and Macou islets	Carenage-Ste Rose	Typical mangrove shoreline	Rivers and channels mouths	
Salinity (PSU)	33.0 ± 1.6	28.8 ± 2.6	p < 0.0001	34.0 ± 0.8	33.5 ± 0.7	29.8 ± 1.9	16.5 ± 7.9	p < 0.0001
Transparency (m)	3.5 ± 0.8	3.3 ± 1.1	N.S.	5.4 ± 1.0	3.4 ± 1.1	2.2 ± 0.7	0.7 ± 0.3	p < 0.0001
Suspended materials (mg/l)	10.5 ± 2.0	12.2 ± 2.6	N.S.	7.9 ± 2.2	10.7 ± 1.6	13.5 ± 3.8	13.1 ± 6.2	N.S. *
Nitrates (μmol/l)	0.1 ± 0.1	0.7 ± 0.3	p < 0.001	0.05 ± 0.04	0.12 ± 0.05	0.53 ± 0.24	1.85 ± 1.02	p < 0.0001

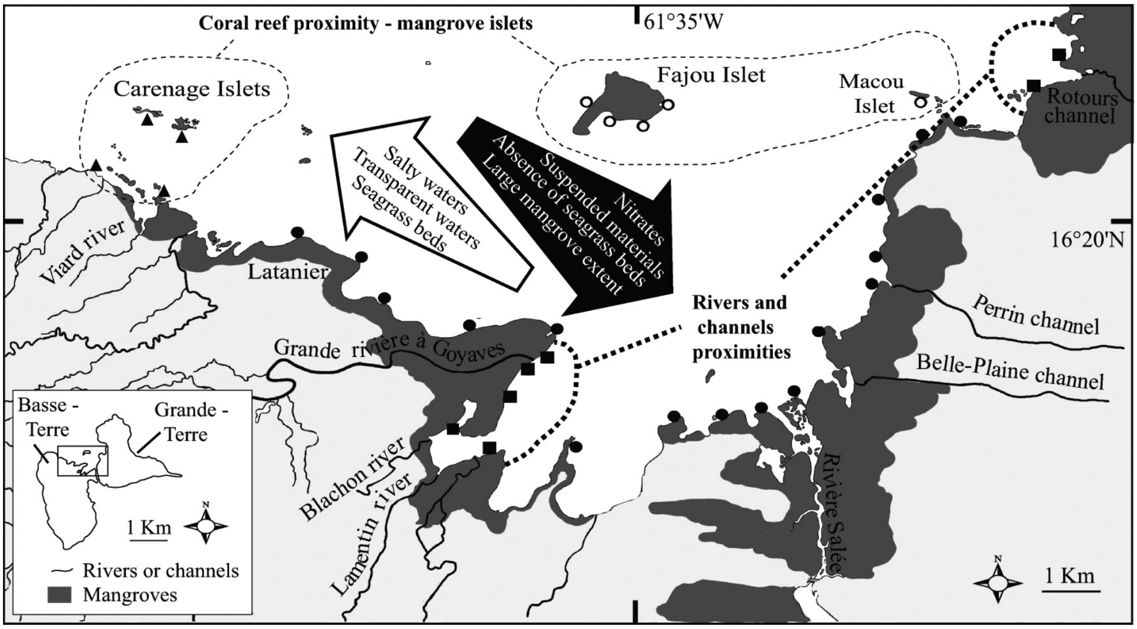

Figure 5. - Representation of the environmental gradients and the four groups of stations identified during the present study. Fajou and Macou islets (○); Carénage-Ste Rose (▲); Typical mangrove shoreline (●); Rivers and channel mouths (■).

mum of 0.5% in abundance and 0.3% in biomass observed in the sites of "Carenage Islets-Ste Rose" (Fig. 6).

DISCUSSION

The diversity, around 100 fish species, observed in the present study is comparable with other studies concerning the shoreline mangroves of the French Antilles: Louis (1983) (111 species); Baelde (1990) (96 species); Louis *et al*. (1992) (87 species); Galzin *et al*. (1982) (64 species).

Around 35% of the variation in the mangrove fish distribution in the GCSM Bay can be explained by environmental and spatial variables. As in the present study, several authors highlighted the relatively high amount of unexplained variation (between 40% to 70%) in the fish distribution (Borcard *et al*., 1992; Costa de Azevedo *et al*., 2007), suggesting that other unmeasured factors (abiotic, biotic) may have an influence on mangrove fish assemblages. Borcard *et al*. (1992) noted that this part of unexplained variation could also be due to the effect of stochastic fluctuations naturally present in the species data sets. However, the several environmental variables found to be significant in the present research can still be considered as important in the structuring of mangrove fish assemblages.

In the GCSM Bay, mangrove fish communities were structured along a coast-seawards terrestrial gradient, defined by physical and chemical factors (salinity, water transparency, suspended materials and nitrates) and spatial variables (reef or river proximities, mangrove extent, presence or absence of seagrass beds).

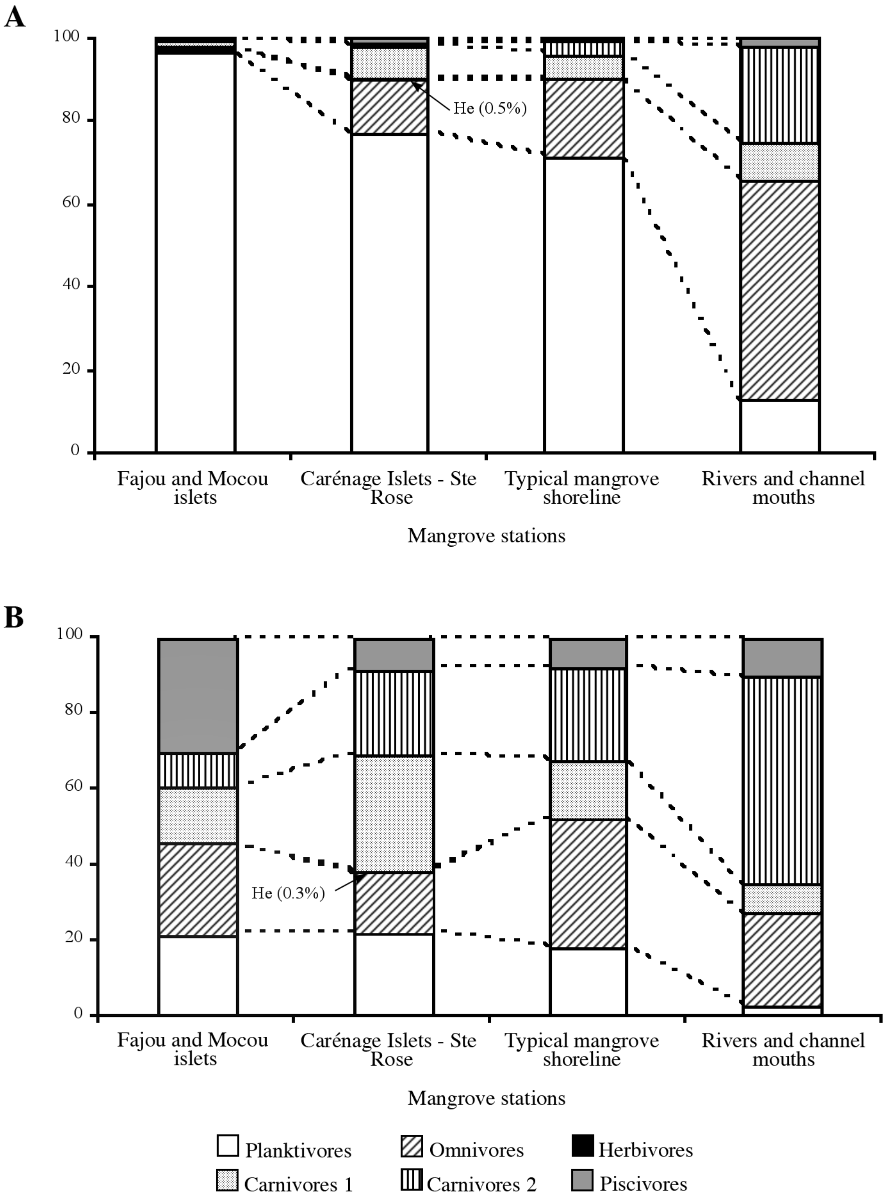

Figure 6. - Structure of trophic categories in the four groups of stations identified by hierarchical analysis (Fig. 3) and represented in figure 6: Fajou and Macou islets (○), Carénage-Ste Rose (▲), Typical mangrove shoreline (●), Rivers and channel mouths (■). The data are expressed in abundance (**A**) and biomass (**B**). He, herbivorous fishes.

Salinity is often evoked as an important variable structuring the mangrove fish assemblages. Most of the fishes present in that ecosystem can tolerate salinity fluctuations. This physiological tolerance is species-specific and salinity gradient may have an influence on fish distributions (Blaber, 2002; Serafy *et al.*, 2003). In the present study, salinity represents an important factor structuring fish communities in the mangrove shoreline. Indeed, reef fish species are present in mangrove islets with near marine salinities (33-34) and resident mangrove species are observed near river mouths stations where the water salinity decreases to 16 due to freshwater inputs. The variation in salinity between the two seasons can also explain the presence during the dry season of a reef fish community in the mangrove islets of Carénage-Ste Rose that are not observed in the wet season when freshwater discharges from rivers decreased the salinity. This trend was also observed by Ley *et al.* (1999) and Serafy *et al.* (2003), who noted distinct fish assemblages in Florida, with mangrove resident euryhaline fish species (Tab. I), which are abundant in mainland mangroves and reef fish species in mangrove habitats having near-marine salinities. However, the range of salinity values must be wide enough to have an influence on fish assemblages. Bouchereau *et al.* (2008) did not observe any influence of salinity in an enclosed mangrove lagoon where salinity ranged between 30.8 and 35.7. By contrast, in the present study, the values fluctuated between 5.8 and 36.5. Moreover, in the present study, several fish species were not significantly associated to a group in the clustering analysis and seemed to occur in different habitats (mangrove, seagrass beds, coral reefs) without specific interactions with environmental variables. This fact can be explained by the ecology of these different fish species. Firstly, some of them sheltered in the shallow and turbid waters in mangroves during their juvenile phase (Lutjanidae, Carangidae, Apogonidae), highlighting the important role of nursery of this habitat. Secondly, that ecosystem can be used as a feeding area for fishes consuming mangrove Invertebrates (Mugilidae, Gerreidae, Lutjanidae) and for piscivorous species (Muraenidae, Megalopidae, Sphyraenidae) foraging on fish present in mangrove.

Another important factor affecting fish distribution is turbidity, which can be related in the present study to the suspended materials and water transparency variables. This factor can affect fish distribution through the species-specific tolerance towards turbidity, as experimented by Cyrus and

Blaber (1987). Moreover, turbid waters are known to provide shelters for juvenile fishes by reducing predation and may explain the abundance of these fishes in coastal waters (Blaber and Blaber, 1980; Robertson and Blaber, 1992).

Some researchers have pointed out the relationships between nitrate concentrations and mangrove fish community structure (Pinto, 1987; Singkran and Sudara, 2005). These authors related higher concentrations of nitrates to terrestrial fertilizers from river runoff, which can also explain the increase of nitrates values observed in the present study from seaward stations to river mouth sites (Tab. II). Moreover, in the present study, omnivorous species are numerically preponderant near rivers, suggesting that nitrates inputs increased the productivity in these stations. This trend was also highlighted in a Mexican mangrove lagoon by Flores-Verdugo *et al*. (1990) who observed an increase in the abundance of detritivorous and omnivorous fishes during the wet season reflecting higher productivity and flushing of organic matter in the lagoon from rivers and terrestrial runoffs.These findings confirm the fact that, at a regional scale, fish assemblages are mainly influenced by the hydrology, diversity and structure of their habitats (Blaber, 2007).

In assessing the relative importance of environmental descriptors, spatial, physical and chemical descriptors explained the largest amount of the variation present in mangrove fish distribution (29.6%) while the seasonal effect is less important (2.9%). The same trend was observed for fish communities in a Brazilian estuary with a spatial structure of environmental variables (equivalent to physical and chemical factors) and that both species and these environmental factors presented a similar spatial structure (Costa de Azevedo *et al.,* 2007). The relative importance of spatial gradients of physical and chemical variables compared to seasonal influence was also found to be significant in other studies undertaken in coastal lagoons in Mexico (Ramos Miranda *et al.,* 2008), Brazil (Costa de Azevedo *et al.,* 2007) or Argentina (González Castro *et al*., 2009).

Moreover, several authors have argued that biotic factors such as food availability influence fish distributions (Nagelkerken *et al.,* 2001; Serafy *et al*., 2003). The structure of fish feeding guilds observed in the GCSM among mangrove habitats confirmed this trend. In the present study, plankton feeders and piscivores dominate in abundance around mangrove islets, located near the barrier reef, whereas omnivores and second order carnivores are preponderant respectively in number and biomass near the coast. The preponderance of planktivorous fishes around mangrove islets can be due to the higher values of water transparency and low sedimentation rates in these sites located near the barrier reef. Indeed, turbidity can reduce and scatters light and has an influence on the feeding activity of planctivorous fish, which depends on visual cues to feed (Thresher, 1983; Ferreira *et al*., 2004). Moreover, the oceanic influence and the continuous current allow sufficient plankton imports (Davis and Birdsong, 1973).

In the present study, Acanthurids and Scarids juvenile herbivorous fishes are less represented in number and biomass in the fish trophic structure. This trend was also observed in different researches using the same fishing net (capéchade) (Bouchon *et al*., 2004) or other nets (Chaves and Bouchereau, 2004) in mangrove lagoons suggesting that this result reflects the structure of mangrove fish assemblage rather than a bias in the fishing device. Moreover, the fact that these young Acanthurid and Scarid fishes feed more in seagrass beds can explain their low abundance in mangrove ecosystems due to the presence of food items of low values in this habitat (Cocheret de la Morinière *et al*., 2003; Nagelkerken and van der Velde, 2004).

Several authors related the abundance of omnivores and second order carnivores in coastal mangroves, particularly near river mouths, to food availability from mangrove shoreline and rivers inputs (Nagelkerken *et al*., 2001; Chaves and Bouchereau, 2004), Higher proportions of first order carnivores in the western part of the Bay (Carenage-Ste Rose islets) may be linked to a greater abundance of benthic Invertebrates on mangrove prop-roots, as suggested by Laegdsgaard and Jonhson (2001) or in adjacent seagrass beds by Nagelkerken *et al*. (2001). This high proportion of first order carnivores, in opposition with the low rate of herbivores, strongly suggests the predominance of a detritus based food web in the mangrove ecosystem (Odum and Heald, 1975).

Thus, these differences observed in the trophic categories distributions suggested that food availability is also an important factor in the structure of the mangrove fish communities in addition to physical, chemical and spatial descriptors.

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